INHERITANCE OF LEFT–HANDEDNESS[1]

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Introduction.—The fact that left-handedness "runs in families" has probably attracted the attention of many observers, yet the method of inheritance has not been fully studied. Many people imagine the condition to depend entirely upon training or imitation. There is thus much of guesswork concerning the true nature of the condition.

Literature.—A considerable bibliography of left-handedness has recently been cited by Professor H. E. Jordan.[2] Most of his references are, however, to articles of little value, especially since nearly all of them were written previous to the modern period of genetic study. Professor Jordan puts forth the tentative opinion that left-handedness is a recessive character. Unfortunately the data which he presents consist chiefly of a few selected pedigrees from which the reader can obtain very little information. He suggests more than once that some of his cases are examples of the spontaneous appearance of left-handedness in a family. If such spontaneous development were so frequent the whole population would, in a few generations, be left-handed. The appearance of a left-handed child in a family without left-handed ancestors for three or four generations is not to be considered remarkable, for this is the way in which recessive characters frequently behave.

Method of Obtaining Data.—At the beginning of a course of lectures on heredity in the University of Colorado in 1911 I distributed papers calling for informa-

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[1] An earlier paper, entitled ''Mendelian Proportions and the Increase of Recessives,'' which grew out of my studies on inheritance of left-handedness was published in the AMERICAN NATURALIST, Vol. XLVI, pp. 344–351, June, 1912.

[2] *Breeders' Magazine,* Vol. II, pp. 19–29 and 113–124, 1911.

tion from the students in regard to right- and left-handedness in their own families or in other families with which they might be quite familiar. Each student noted down the parents and every child in the family. Since the students who reported are from nineteen to twenty-five years of age, the probability is that their families are now complete as to the number of children. Similar data were collected from another set of students in 1912. In addition to these collections of statistics, I have also studied the affection in a family of four generations, including about thirty people. Since this material offers nothing especially different from that gathered from the students, I have not included it in the present study.

TABLE I

Statistics of Parents and Children

	Number	Per Cent. Observed	Per Cent. Expected $4RR:4Rr:rr$	Per Cent. Expected $9RR:12Rr:4rr$
Total parents..........	610			
Right-handed parents...	561	91.94	89.99	84.00
Left-handed parents....	49	8.06[3]	11.11	16.00
Total children.........	1,130			
Right-handed children ..	953	84.34	89.99	84.00
Left-handed children....	177	15.66[3]	11.11	16.00

Value of Different Data.—Since the young people from whom the information was obtained would be much more likely to know of left-handedness among their brothers and sisters than in their parents, the reports for children are probably more accurate than those for parents. It is easy to see how a child would report a parent as right-handed unless the person were very definitely left-handed. A child would not know about the early history of his father or mother. On comparison of the number of left-handed individuals among parents and children left-handedness seems to be about twice as common among the children. This is, of course, a manifest absurdity and is

[3] Since the proportion of left-handed children is nearly twice that of the left-handed parents it is evident that left-handedness among the parents is greatly under-reported.

<div align="center">

TABLE II

Statistics of Families

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	Number	Per Cent. Observed	Per Cent. Expected $4RR{:}4Rr{:}rr$	Per Cent. Expected $9RR{:}12Rr{:}4rr$
Total families......................	305			
Families with both parents reported as right-handed.....................	258	84.59	79.01[4]	70.56[5]
Families reported as having one parent right-handed, the other left-handed.	45	14.75	19.74[4]	26.88[5]
Families reported as having both parents left-handed...............	2	0.66	1.24[4]	2.56[5]
Families reported as having all children right-handed.....................	174	57.05	69.13[4]	59.04[5]
Families with some or all children left-handed..........................	131	42.95	30.87[6]	40.96[7]
Average number of children per family in the population (families 305, children 1,130)....................	3.7			
Average number of children among families showing some left-handed children (families 131, children 548)	4.1			

[4] The expected number of matings of any particular sort, or the matings resulting in particular types of offspring, in a population of $4RR{:}4Rr{:}rr$ may be calculated from the following table:

<div align="center">

1. $4RR \times 4RR = 16$
2. $4RR \times 4Rr = 16$
3. $4RR \times rr = 4$
4. $4Rr \times 4RR = 16$
5. $4Rr \times 4Rr = 16$
6. $4Rr \times rr = 4$
7. $rr \times 4RR = 4$
8. $rr \times 4Rr = 4$
9. $rr \times rr = 1$

$\overline{81}$

</div>

Matings 1, 2, 4 and 5 have both parents right-handed; adding $16 + 16 + 16 + 16 = 64 \div 81 = 79.01$ per cent. Matings 3, 6, 7 and 8 are each of a right-handed and a left-handed parent. Mating 9 is of two left-handed parents; this type may be expected once in 81 times, or $1 \div 81 = 1.24$ per cent. Only right-handed children will appear in matings 1, 2, 3, 4 and 7; left-handed children are to be expected in 5, 6, 8 and 9. These last make $16 + 4 + 4 + 1 = 25 \div 81 = 30.87$ per cent.

[5] The expected number of matings of a particular sort, or the matings resulting in particular types of offspring, in a population of $9RR{:}12Rr{:}4rr$ may be calculated as suggested in the previous footnote. Here it is necessary to use the following table:

<div align="center">

1. $9RR \times 9RR = 81$
2. $9RR \times 12Rr = 108$
3. $9RR \times 4rr = 36$
4. $12Rr \times 9\dot{R}R = 108$

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to be accounted for as just stated. Probably the most valuable parts of the statistics are the figures showing families with left-handed children and also the total number of left-handed children in the population.

Natural and Acquired Left-handedness.—Most right-handed people can be taught to use the left hand for many purposes, and conversely left-handed people may learn to write and perform various acts of skill with the right hand. But aside from these rather unusual cases there are many individuals who are naturally right-handed and do most of their work with the right hand. Others are left-handed by nature. Left-handedness seems to be connected with a more highly developed condition of the right cerebral hemisphere. Evidence in support of this view is found in a number of cases of aphasia connected with left hemiplegia. The left motor area of the cortex, as is well known, is associated with speech in most individuals. Hence a lesion of this area results in aphasia and paralysis of the right side of the body. When similar

$$5.\ 12Rr\ \times\ 12Rr\ = 144$$
$$6.\ 12Rr\ \times\ 4rr\ =\ 48$$
$$7.\ 4rr\ \times\ 9RR\ =\ 36$$
$$8.\ 4rr\ \times 12Rr\ =\ 48$$
$$9.\ 4rr\ \times\ 4rr\ =\ 16$$
$$\overline{625}$$

[6] Only in the following matings could left-handed children appear:

$$4Rr \times 4Rr = 12 \text{ right-handed, 4 left-handed}$$
$$4Rr \times\ \ rr =\ 2 \text{ right-handed, 2 left-handed}$$
$$rr\ \times 4Rr =\ 2 \text{ right-handed, 2 left-handed}$$
$$rr\ \times\ \ rr =\ 0 \text{ right-handed, 1 left-handed}$$
$$\overline{16} \qquad\qquad \overline{9}$$

The children in these families would then be expected in the ratios of 16 : 9, or 64 per cent. right-handed, 36 per cent. left-handed.

[7] Only in the following matings could left-handed children appear:

$$12Rr \times 12Rr = 108 \text{ right-handed, 36 left-handed}$$
$$12Rr \times\ 4rr =\ 24 \text{ right-handed, 24 left-handed}$$
$$4rr\ \times 12Rr =\ 24 \text{ right-handed, 24 left-handed}$$
$$4rr\ \times\ 4rr =\ \ 0 \text{ right-handed, 16 left-handed}$$
$$\overline{156} \qquad\qquad \overline{100}$$

The children in these families would then be expected in the proportion of 156 right-handed to 100 left-handed, or 61 per cent. right-handed and 39 per cent. left-handed.

TABLE III

Statistics of Families Reported as Having Both Parents Right-handed

	Number	Per Cent. Observed	Per Cent. Expected [8] $4RR:4Rr$ $:rr$	Per Cent Expected [8] $9RR:12Rr$ $:4rr$
Total families in the group..........	258			
Families within this group having all children right-handed............	165	63.95[9]	75.00[10]	67.35[11]
Families within this group having some children left-handed.............	93	36.05[9]	25.00[10]	32.64[11]
Total children in the group..........	953			
Right-handed children reported in the group...........................	837	86.74	93.75[12]	91.84[13]
Left-handed children reported in the group...........................	116	13.26	6.25[12]	8.16[13]
Children in those families in which all children are right-handed..........	555	58.24[9]	75.00[10]	67.35[11]
Children in those families in which some children are reported as left-handed......................	398	41.76[9]	25.00[10]	32.65[11]
Right-handed children in those families in which part of the children are left-handed......................	282	70.85[9]	75.00	75.00
Left-handed children in those families in which part of the children are left-handed....................	116	29.15[9]	25.00	25.00

[8] See footnotes 4 and 5 to Table II.

[9] The figures show that some of the alleged right-handed parents are really left-handed.

[10] The population considered in this table is made up of matings 1, 2, 4 and 5 given in footnote 4 to Table II, thus:

$$1.\ 4RR \times 4RR = 16$$
$$2.\ 4RR \times 4Rr = 16$$
$$4.\ 4Rr \times 4RR = 16$$
$$5.\ 4Rr \times 4Rr = 16$$
$$\overline{64}$$

Obviously, only mating 5 will show left-handed children. This constitutes $16 \div 64 = 25$ per cent. of the families.

[11] The entire population considered in this table is made up of matings 1, 2, 4 and 5 in footnote 5 to Table II, thus:

$$1.\ 9RR \times 9RR = 81$$
$$2.\ 9RR \times 12Rr = 108$$
$$4.\ 12Rr \times 9RR = 108$$
$$5.\ 12Rr \times 12Rr = 144$$
$$\overline{441}$$

The families showing left-handed children would be only those in mating 5. This constitutes $144 \div 441 = 32.65$ per cent.

[12] The only left-handed children will be in mating 5, viz.: $4Rr \times 4Rr$. They will constitute one fourth of the children in this mating, or one sixteenth of all the children $= 6.25$ per cent.

[13] The only left-handed children will be in mating 5, viz.: $12Rr \times 12Rr$. They will constitute one fourth of the children in this mating. Hence: $\frac{1}{4} \times 144 \div 441 = 8.16$ per cent.

lesions of the right cerebral cortex result in paralysis of the left side and also in aphasia, it is sometimes found that the persons thus affected were naturally left-handed. I am informed by my colleague, Dr. O. M. Gilbert of the department of medicine of this university, that this connection of left-handedness with a speech center on the right side of the cortex is well attested.

A certain number of persons consider themselves to be ''ambidextrous'' and claim that they are not naturally either right-handed or left-handed. It is, however, difficult for one to know his own original condition with regard to the use of the hands, since in most homes the child is taught early the use of the right hand in taking up a spoon or cup. I suspect that the ''ambidextrous'' persons are really left-handed by nature.

Mendelian Explanation of Heredity of Left-handedness.—A study of the accompanying tables will suggest that left-handedness is a Mendelian recessive. It belongs to that group of characters which may show themselves in families where neither parent is affected, and sometimes in families with no affected ancestors for a number of generations. In the 305 families there are only two reported as having both parents left-handed. If the condition is a Mendelian recessive the children in these families should all be left-handed. According to the report, however, one child is right-handed. Of course it is possible that one of the parents was by nature right-handed. Possibly some heterozygous (simplex) persons may easily learn to use the left hand.

Presentation of Material.—The material collected has been classified in such manner that it can be made use of by others who may be studying the subject. In some of the tables I have indicated the expected percentages if the population were to consist of the three Mendelian types of individuals in the following proportions, viz.:

$$(a)\ \ 4RR:\ 4Rr:\ rr,$$
$$(b)\ \ 9RR:12Rr:4rr.$$

TABLE IV

BOTH PARENTS REPORTED AS RIGHT-HANDED, BUT WITH SOME OF THE
CHILDREN LEFT-HANDED (FAMILIES 93, RIGHT-HANDED CHILDREN
138, LEFT-HANDED CHILDREN 116).[14]

Name of Person Reporting	Right-handed Children	Left-handed Children	Name of Person Reporting	Right-handed Children	Left-handed Children
Ahr.........	2	1	Max........	1	1
Ba.........	0	1	Mer (a).....	1	1
Bar........	3	1	Mer (b).....	2	1
Bat........	3	1	Milb........	1	1
Ben.......	3	1	Mill. L......	3	1
Br. F.......	1	1	Mill. W.....	6	2
Br. H......	3	1	Mur........	4	1
Br. N......	2	3	N..........	8	1
Bu........	3	1	Ol..........	4	1
Bur........	2	1	Ow........	1	1
Chr........	3	1	Pe..........	9	3
Con.......	1	1	Po..........	2	1
Cou.......	1	1	Pu.........	7	1
D.........	0	1	Re........	1	1
Don.......	4	1	Rid (a).....	2	2
Dou.......	5	1	Rid (b)......	0	1
Ed........	4	1	Rid (c)......	2	2
F (B)......	3	1	Ro.........	4	1
F (C)......	5	1	Roberts.....	6	2
Fl..........	1	2	Rbtn (a)....	4	1
Fur........	1	1	Rbtn (b)....	2	1
Ga........	4	1	Rbsn.......	2	1
Gi.........	3	2	Sa..........	6	3
Goo (a).....	1	1	Salb........	4	2
Goo (b).....	2	2	Sc (M)......	3	1
Gr.........	1	3	Sc (P)......	1	1
Ha (P)......	5	2	Schm.......	6	2
Har........	2	1	Shee.......	3	2
He........	2	1	Sheld......	1	1
Hi.........	2	1	Sm........	0	1
Hu........	2	1	Smi (B).....	4	1
Hun........	3	1	Smoth......	3	1
Is.........	8	1	Spra.......	2	1
J (M)......	3	1	Stream......	1	1
J (R)......	6	2	Sul.........	3	1
Joh........	3	2	T..........	3	1
Jon........	1	2	Tay (R).....	7	1
Ka........	3	1	Tenn.......	2	1
Kei........	3	1	Terw.......	3	1
Kel........	5	1	Warn.......	2	1
Ken.......	3	1	Web (H)....	4	1
L..........	4	1	Weim.......	1	1
Li..........	7	2	Wh (E).....	2	1
Mac........	5	1	Wh (H).....	2	1
McNab.....	4	1	Wilh........	4	1
McPh......	4	1	Wr.........	4	1
Ma........	3	1			
				138	116

[14] The percentage of left-handed children is 45.67. According to Mende-
lian rules the expectation is 25 per cent. As noted before it is apparent that
many of the parents reported as right-handed are really left-handed. Hence
the large excess of left-handed children.

In the above ratios RR is pure right-handed, Rr is heterozygous right-handed and rr is left-handed. I have taken these particular proportions because they are stable and they approximate to a degree the actual condition in the population studied. As is noted in the table, the number of left-handed persons is probably greater than the reports indicate. Some families reported as having both parents right-handed evidently belong with the group of one left-handed and one right-handed. Some reported in this latter group belong, no doubt, with those having both parents left-handed.

TABLE V

ONE PARENT RIGHT-HANDED, THE OTHER LEFT-HANDED

A. Right-handed Parent Evidently Heterozygous (Families 36, Right-handed Children 88, Left-handed Children 55).

Name of Person Reporting	Right-handed Children	Left-handed Children	Name of Person Reporting	Right-handed Children	Left-handed Children
Ba.........	1	1	Li (b)......	1	1
Bi.........	2	1	McD........	2	1
Br.........	2	1	McF........	3	1
Bra........	3	1	McK.......	3	1
Ca.........	3	4	Mal........	2	1
Ch.........	2	2	Mil........	2	1
Cu.........	4	2	Mit........	3	2
D'A........	0	1	Ols (a)......	1	1
Di.........	2	1	Ols (b)......	1	2
Fra........	4	1	Or.........	0	1
Fre........	1	1	Re.........	3	1
H (d)......	4	3	Ri.........	2	1
He.........	4	1	Str........	2	1
Hea........	2	3	Wa (a)......	2	1
Hi.........	2	2	Wa (b)......	1	1
Ho.........	5	2	Web........	2	1
Kei........	5	3	Wei........	5	2
Li (a)......	2	2	Wil........	5	3
				88	55

Fecundity of Left-handed Families.—It is well known that in certain species of animals races showing particular recessive traits have less vitality and perhaps less reproductive ability than the ordinary members of the species. From the studies herein recorded, especially in Table II, it is seen that the left-handed families are quite as fertile as the normal ones.

Summary.—The foregoing pages are given to a study of left-handedness among 610 parents and 1,130 children, the data being collected from students at the University of Colorado. It is concluded that left-handedness is a Mendelian recessive. The condition probably exists in about one sixth of the population. A suggestion is made that the three Mendelian types of individuals may exist in some such proportion as 9 *homozygous right-handed*: 12 *heterozygous right-handed*:4 *left-handed*.

B. *Right-handed Parent Probably Homozygous (Families 9, Right-handed Children 27, Left-handed Children 0).*

Name of Person Reporting	Right-handed Children	Left-handed Children	Name of Person Reporting	Right-handed Children	Left-handed Children
Ba.........	5	0	Nau........	2	0
Be.........	4	0	Pi..........	3	0
Bl..........	1	0	Spr.........	2	0
Du.........	4	0	Sto.........	3	0
Mi.........	3	0		27	0

TABLE VI

BOTH PARENTS REPORTED AS LEFT-HANDED

Name of Person Reporting	Number of Right-handed Children	Number of Left-handed Children
McN	1	2
P	0	4
	1[15]	6

[15] Mendelian expectation requires that all the children of these families be left-handed. It is possible that one of the parents in the McN family was naturally right-handed and that the left-handedness was only acquired. If this is not the case then there seems no explanation to offer for the appearance of the right-handed child.